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Spatial synchrony is related to environmental change in Finnish moth communities

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Abstract

Spatially distinct pairs of sites may have similarly fluctuating population dynamics across large geographic distances, a phenomenon called *spatial synchrony*. However, species rarely exist in isolation, but rather as members of interactive communities, linked with other communities through dispersal (i.e., a metacommunity). Using data on Finnish moth communities sampled across 65 sites for 20 years, we examine the complex synchronous(anti-synchronous) relationships among sites using the geography of synchrony framework. We relate site-level synchrony to mean and temporal variation in climatic data, finding that colder and drier sites – and those with the most drastic temperature increases – are important for spatial synchrony. This suggests that faster warming sites contribute most strongly to site-level estimates of synchrony, highlighting the role of a changing climate to spatial synchrony. Considering the spatial variability in climate change rates is therefore important to understand metacommunity dynamics and identify habitats which contribute most strongly to spatial synchrony.

Introduction

Populations fluctuate through time [**?**], and a central goal of population ecology has been to understand, quantify, and relate these fluctuations to fundamental ecological processes such as predation [**?**], extinction risk [**?**], and environmental forcing [**?**]. Scaling processes acting on single populations, the study of spatial synchrony attempts to quantify how population time series are related [**?** **?** **?**]. There are three main putative drivers of spatial population synchrony. First, spatially autocorrelated environmental conditions can result in synchronous populations even when populations are thousands of kilometers away [**?**]. This pheonomenon – often referred to as the *Moran effect* [**?**] – is well-supported by both empirical [**?** **?** **?** **?** **?**] and theoretical [**?** **?**] research. Second, dispersal between populations may synchronize paired populations [**?** **?** **?**]. Lastly, a mobile shared enemy capable of attacking paired populations may create synchronous population dynamics [**?** **?** **?** **?**], as can interactions with other synchronous species. For instance, a parasite species with pronounced seasonal variation may influence local host population dynamics [**?** **?**], as well as the synchrony between host populations [**?**]. These mechanisms, whether in isolation or combined, drive the resulting spatial synchrony. Disentangling the relative importance of these three mechanisms is an important question in ecology, as synchronous populations may be more likely to go extinct at the same time [**?** **?**], suggesting an association between synchrony and (meta)population stability [**?** **?**].

Identifying which local populations are *most* synchronous – or contribute most to spatial synchrony – may provide insight into the relative importance of habitat patches to the resulting spatial population dynamics. For instance, conservation or management actions designed to reduce or enhance synchrony, respectively, may benefit from targeting specific local populations. One way to assess the importance

of individual populations to spatial synchrony across the entire spatial network is by combining the *geography of synchrony* approach [**?**] with measures from graph theory. Similar approaches have also been developed to examine variation in site-level contributions to spatial synchrony [**?** **?**]. The *geography of synchrony* approach – specifically with respect to the incorporation of graph theory – builds a spatial network of local populations, which are connected to other populations based on their degree of synchrony(anti-synchrony), which can be measured given time series or across a rolling window. This spatial network can then be analyzed using graph theoretic measures such as *centrality*, which quantifies the importance of each local population to the topological structure of the entire spatial network (i.e., metapopulation) [**?**]. This method has been used previously to examine the importance of particular areas in human cortical networks [**?**], site-level contributions to synchrony of Bovine Tuberculosis incidence [**?**], and large-scale spatial variation in vegetation [**?**] and marine phytoplankton [**?**] synchrony.

Estimating site-level contributions to spatial synchrony allows an examination of the associated spatial and environmental variables. More traditional approaches to the analysis of spatial synchrony use matrix regressions [**?** **?**] or are based on pairwise data, which are incredibly useful and powerful, but do not provide a single measure for each site [**?**]. However, site-level measures incorporate information on all of the synchronous (anti-synchronous) interactions with other sites, creating a single measure which can be related directly to environmental or spatial gradients. Further, in addition to relating mean environmental conditions to synchrony estimates, the rate of change in environmental conditions may be important to temporal variation in the strength of spatial synchrony. For example, mean environmental conditions could be unrelated to site-level contributions to spatial synchrony, while the rate of environmental change may show a clear

signal. This would suggest that sites contributing strongly (or weakly) to spatial synchrony are undergoing different rates of environmental change relative to other sites. Importantly, this could create a situation where the most important sites to driving spatial synchrony are also undergoing the most rapid environmental changes, with the potential to either reduce or enhance spatial synchrony in the future. While climate-induced synchrony is a fairly well-studied phenomenon [**? ? ? ?**], studies incorporating spatial differences in the rate of environmental changes and the resulting potential impacts are not yet developed.

In addition, species rarely exist in isolation, but rather as part of a larger community of interacting species. Combining data on multiple species may provide insight into interspecific differences in synchrony, which could then be related to dispersal ability, competition, or sensitivity to environmental pressures. Studies focused on the drivers of spatial synchrony of a single important species are still quite valuable, but community-level data offer a number of intriguing research possibilities. First, synchrony can be calculated using the fluctuations in density of the entire community. Competition and ecological drift may create fluctuations in single species dynamics which become undetectable when considering community density. Second, synchrony can be calculated for each species, and the importance of spatial locations to synchrony could be compared among species. That is, interspecific differences in species environmental tolerances (i.e., niches), spatial distribution, or life history traits may result in differences in the relative importance of each site to spatial synchrony. Lastly, synchrony networks could be formed for each species (as above), and then combined together to form one ensemble synchrony network. Links between sites then become the mean synchrony for all species shared between those two sites (i.e., communities), potentially removing some of the influence of demographic stochasticity on estimates of synchrony.

Here, we use data on Finnish moth communities surveyed across 65 sites for 20 years (1993-2012) to examine the spatial variability in local site relative importance to spatial synchrony networks. The spatio-temporal structure of the data allow estimation of the spatial variation in sites driving spatial synchrony. Using these extensive data, we create a single synchrony network, taking the mean synchrony value for all shared species between any two sites as a measure of synchrony. Using measures from graph theory, we demonstrate spatial variability in the relative importance of sampling sites to driving spatial synchrony. Further, we examine how mean and temporal variation in temperature and precipitation relate to site-level importance to spatial synchrony. We found that sites more important for spatial synchrony tended to be colder and drier. These sites corresponded to more northern locations, where temporal patterns in temperature change are also stronger. This suggests that currently cold sites – which are warming more quickly – are also those sites which contribute strongly to synchrony networks. Together, our findings provide a demonstration of the utility of the *geography of synchrony* approach to community data, highlight the clear existence of spatial variation in the temporal environmental change and site-level contributions to spatial synchrony, and identify a clear relationship between the importance that a site plays in maintaining spatial synchrony and both the mean and temporal variation in climatic conditions.

Methods

Moth communities of Finland

Data on moth species abundances were gathered as part of the Finnish national moth monitoring scheme (`Nocturna`; an overview provided in [**?**]). Moth communities were sampled using light traps ("Jalas" model) – using either 160W mixed

light or 125W Mercury (Hg) vapour bulbs [**?** **?**] – located mainly in forested areas, and run every night from early spring to late autumn (i.e., between April and October). Every week (or occasionally every other week), light traps were emptied and moth specimens were counted and identified to species by voluntary observers. Quality control of the data and cross-checking of moth identifications was carried out by the coordinating team at the Finnish Environment Institute (SYKE). A total of 208 trap sites were included in the monitoring network between 1993 and 2012. We examined a subset of 65 traps sampled in at least 8 years during the study period, so as to minimize temporal gaps in the community time series, as these gaps could influence spatial synchrony estimation. Pairs of sites were not necessarily sampled at the same time, and the temporal overlap between sites may influence the estimation of spatial synchrony, as estimates of synchrony required both species to be sampled at a particular sampling event. To account for this effect, we use the number of sampling events at each site as a covariate in our models (more information given below, and see Figure **??**). This had no effect on our overall findings. Overall, these data cover all species of Macroheterocera (i.e., macro-moths) and the families Hepialidae and Cossidae, and consist of over 4.12 million individual moths belonging to 731 species.

Quantifying environmental change

Data on monthly mean precipitation and temperature between 1990 and 2013 was obtained from the Finnish Meteorological Institute (an extension of the data from [**?**]). We measured both the mean values and the temporal change in precipitation and temperature for each 1 km^2 grid cell for the whole of Finland. Temporal change was quantified using Spearman's correlations of environmental conditions and time to account for non-linear environmental changes over time. This created a gridded map of the temporal change in precipitation and temperature for all of Finland

(see Supplemental Materials), and data for each sampling site was extracted from this gridded map.

Geography of synchrony

To examine the contribution of each site to spatial synchrony at the community level, we first calculated time series correlations among all pairs of sites and each sampled moth species (Figure **??**), following the *geography of synchrony* approach [**?**]. We used the annual mean moth abundances at each site, to account for the strong seasonality in moth species dynamics. However, we explore the effect of temporal sampling scale in the Supplemental Materials, finding equivalent results when using a monthly sampling scale.

Population dynamics may be synchronous (positive correlation) or anti-synchronous (negative correlation). Synchrony between sites was estimated using Pearson's correlation coefficients, where links between sites were only considered if they were significantly ($\alpha < 0.05$) different from zero. This addresses potential issues of phase-locking and cyclic dynamics, as sites undergoing strong coupled interactions like phase-locking would have a strongly positive relationships. Further, we removed one species known to dominate communities in terms of abundance during certain years in the more northern sites, which is known to exhibit multi-annual population cycles, and found no change to our results (see Supplemental section entitled "Removal of a known cyclic species"). Any pair of sites will have a number of time series correlations equal to the number of shared species between sites. To quantify average synchrony between any two sets of sites, we separated the positive and negative synchrony values into two networks, combining species-level networks by taking the mean time series correlation for all shared species between any pair of sites as a measure of positive or negative synchrony. This produced

two networks: a synchrony network containing positive mean associations between sites, and an anti-synchrony network containing negative mean associations. We considered the absolute value of the correlation coefficient between pairs of sites as a measure of spatial synchrony. These networks were analyzed separately, then site-level contributions to synchrony (anti-synchrony) were combined to estimate overall contribution of a site to spatial synchrony.

To estimate the contribution of each sampling site to synchrony (and anti-synchrony) networks, we calculated two *centrality* indices, which measure the topological importance of a site in the spatial network based on the number and weights of the associations between sites. The site-level contribution to the network was estimated as the difference between the centrality values in the synchrony network and the anti-synchrony network.

The two measures we used were strength (also referred to as weighted degree centrality) and eigenvector centrality. Strength was estimated as the sum of link strength (i.e., mean synchrony between a pair of sites) for each site standardized by dividing the total number of links with other sites [**?**]. We remove this standardization by the total number of links with other sites in the Supplemental Materials, finding that it does not influence our results. Eigenvector centrality is a related measure which uses information on the entire network structure to estimate importance of each node in the network. This approach is used by Google's PageRank algorithm, which quantifies the importance of a node as a function of connections with other important nodes. While often related (see Supplemental Materials), the two measures incorporate different levels of information, and therefore can estimate different aspects of site importance in the synchrony networks. That is, strength captures the importance of a site given immediate local connections, while eigenvector centrality measures the importance of a site based on the

connections of those local connections [**?** **?**], providing a more regional estimate of site importance which considers connections across the entire spatial synchrony network.

There are many factors which may influence these centrality measures. Depending on the distribution of synchrony values, sites sharing more species may have higher mean synchrony values on average. This would make synchrony values sensitive to the number of shared species between two sites, or to variation in sampling effort. To address these effects, we considered the association betwen sites to be the mean synchrony or anti-synchrony value for all shared species, standardized estimates of site importance (centrality) by the total number of synchronous or anti-synchronous links (i.e., the number of other sites each site had significant synchronous or anti-synchronous associations with; see Supplemental Materials), and incorporated sampling effort into our models (as described below).

Relating synchrony to environmental change

The importance of sites to spatial synchrony may be associated with environmental conditions. We used linear mixed effects models – specifically the *R* package lme4 [**?**] – to relate site-level contribution to spatial synchrony (centrality values) to both the mean and temporal variation in precipitation and temperature. Spatial autocorrelation was controlled by incorporating a Gaussian spatial correlation random effect. Some sites were not sampled at each sampling event, due to severe weather conditions or other logistical challenges. This variation in sampling effort may influence the resulting synchrony values and corresponding site-level centrality values. To examine the importance of this effect on site-level centrality, we incorporated the number of sampling events as a fixed effect. This results in two models, depending on whether site-level contributions to spatial synchrony were

quantified using strength or eigenvector centrality.

Data and code to reproduce the analyses described are provided at `https://doi.org/10.6084/m9.figshare.9036941`.

Results

Synchrony networks

Across our 65 sampling sites, we calculated pairwise synchrony for every possible combination of sites, building up networks of spatial synchrony. Each link in the network was defined as the mean synchrony for all species shared between the two sites. From this, we created two spatial networks, one containing significant ($\alpha = 0.05$) positive mean associations between pairs of sampling sites, and the other containing the significant negative mean synchrony values (Figure **??**). Centrality values for each node in the synchrony network provided estimates of site-level contributions to spatial synchrony. We find similar spatial patterns in site importance to synchrony for both centrality measures considered (strength and eigenvector centrality), where more northern sites contributed more strongly to spatial synchrony compared to more southern sites (Figure **??**). Defining the contribution of each site to synchrony without standardizing by the number of links did not change our overall findings (see Supplemental Material). Finally, we examined the relationship between site contributions to synchrony and anti-synchrony in the Supplemental Materials, finding that sites contributing strongly to spatial synchrony also contribute strongly to anti-synchrony. This effect may be a function of species richness, but this does not influence our estimates of site-level contributions to overall synchrony, as these values are standardizing by the number of significant correlations linking sites (see Supplemental Materials).

Relating synchrony to environmental change

Northern sites contributed more strongly to spatial synchrony, which might be expected if the spatial distribution of sampling sites was higher in northern latitudes, as synchrony is expected to be greater when distance between sites is small (see Supplemental Materials for exploration of distance decay in synchrony). However, we observe the opposite pattern, with the far more spatially distinct northern sites contributing more strongly to synchrony. Relating the mean values in temperature and precipitation to site synchrony estimates showed that both were negatively related to site-level contributions to spatial synchrony (Table **??**).

Additionally, site-level contributions to the synchrony network (Figure **??**) were positively related to temporal temperature change, but unrelated to precipitation change (Table **??**). This means that sites with lower mean temperature and larger temporal temperature change contribute more strongly to spatial synchrony (Figure **??** and Tables **??** and **??**). Both mean values and temporal variation in climatic conditions were negatively related to one another for both temperature (r = -0.67, t = -7.16, $p < 0.0001$) and precipitation (r = -0.32, t = -2.68, $p = 0.009$), suggesting that warmer and wetter sites correspond to low rates of temporal climatic change. We failed to observe a significant effect of variation in sampling effort among sites (Table **??**), though sampling effort was significantly related to site-level contributions to synchrony in models including mean temperature and precipitation (Table **??**). Finally, our results were robust to the quantification of pairwise links between sites estimated using all species correlation coefficients instead of only significant relationships (see Supplemental Materials). Specifically, the importance of mean temperature to site-level estimates of synchrony remained similar (Table **??**), but the influence of precipitation was not observed in the mean climate models. We discuss this difference further in the Supplemental Materials.

Discussion

We found clear spatial signals in the importance of sampling sites to spatial synchrony across a large latitudinal gradient, with higher site-level synchrony values in more northern sites. Further, we found a clear relationship between the importance of each site in the spatial synchrony network and 1) mean temperature and precipitation and 2) the temporal change in temperature. This suggests that environmental forcing is potentially an underlying mechanism in synchronizing moth population dynamics, and that the unequal spatial distribution of environmental change is disproportionately influencing spatial synchrony of certain areas. Overall, colder and drier sites tend to contribute more strongly to spatial synchrony, linking mean environmental conditions to synchrony estimates. Further, differences in the temperature change may manifest as differences in the importance of sites to promoting spatial synchrony. Together, our results provide a clear demonstration that gradients in temporal change in temperature, but not precipitation, were related to differences in the relative importance of sites to spatial synchrony. Understanding which environmental variables are important to driving spatial synchrony – and the associated rates of change in environmental variables – can provide a clearer understanding of the relative importance of dispersal processes and environmental forcing on spatial synchrony. Finally, identifying which sites contribute most to spatial synchrony – a phenomenon closely related to metapopulation persistence – may aid in conservation and management efforts [**?**], as manipulating the system to reduce spatial synchrony may serve to stabilize metapopulation dynamics.

The approach of examining spatial synchrony networks does not allow us to readily tease apart the relative roles of environmental forcing from the effects of dispersal or predator distributions. Still, it seems unlikely – though not impossi-

ble [**?** **?**] – that a mobile predator could be driving the observed dynamics due to the large spatial extent of the study. However, large ranging migratory bird species that prey on moths could have geographic ranges covering large portions of Finland. Moreover, it seems unlikely that dispersal would be a driver in this case, as a higher degree of synchrony was observed in more northern sites, where distances between sites are larger and dispersal becomes less likely. Further, synchrony was observed between sites at the latitudinal extremes of Finland, spanning a greater distance than dispersal processes would likely influence. Seasonality in moth communities is pronounced, which could produce signals of synchrony as a function of environmental processes (a form of the Moran effect). These short-term seasonality-driven dynamics capture life history variation and phenological events in moth populations, but are perhaps not the appropriate scale for examining spatial synchrony in longer term data. We examined synchrony at the annual timescale in order to remove transient or seasonal population processes. In the Supplemental Materials (Tables **??** and **??**), we analyze moth communities at the monthly timescale, finding qualitatively similar results to the annual timescale. It should be noted that the annual scale does not remove multi-year cyclic behavior, as has been observed in a small number of moth species [**?** **?** **?**], particularly *Epirrita autumnata* (see Supplemental Materials for an analysis where we remove this species).

While previous work on this cyclic Fennoscandian moth species (*Epirrita autumnata*) suggested the existence of spatial clusters of synchrony [**?**]. Such work has focused on understanding the cyclic nature of outbreaks, as large increases in population size can defoliate an area. Taking this further, a set of synchronous moth populations may cause synchronous defoliation across much larger areas, resulting in pronounced effects on forest dynamics [**?** **?**]. Taking a bottom-up

perspective, synchrony in the emergence or abundance of a resource may drive synchronous dynamics in the predator species [**?**]. Relatedly, numerically dominant outbreaking species may drive synchrony by disrupting community dynamics and promoting synchrony in other species through competitive interactions [**?** **?**]. Both of these are potential explanations for the latitudinal variation observed in the importance of each site to the synchrony network, as resource availability and community composition changes with latitude in Finland [**?**]. Disentangling the relative roles of temporal temperature patterns and the role of resource communities is well beyond the scope of the current work, but disentangling the underlying mechanisms driving geographic variation in site-level contributions to synchrony is an important next step. Another clear next step is the continued integration of graph theoretic approaches to networks of spatial synchrony. Measures of entire networks, instead of each node (habitat patch), may provide insight into the organization of modular subcommunities within synchrony networks, or other interesting network structures. Using the *geography of synchrony* approach, and comparing spatial synchrony networks of different taxa, may allow inference into the relative roles of dispersal processes, synchronized resources, environmental forcing, and the influence of mobile predators or parasites.

In addition to elucidating the underlying mechanisms driving spatial synchrony, our results highlight that we must consider the rate at which environments are changing, and the spatial distribution of environmental change, as this will certainly influence relative importance of sites to synchrony networks [**?**]. The significant relationship between the mean and temporal variation in climatic conditions highlights the difficulty in establishing a causal link between synchrony estimates and climatic conditions. It is of great interest that warmer sites contribute less to synchrony networks compared to cold sites, but that these more northern, colder

sites are also becoming warmer at an accelerated rate relative to more southern sites (Figure **??**). Here, we provide a clear demonstration that temporal temperature change over the last twenty years is strongly related to spatial synchrony in moth communities, with sites in areas of greater environmental change (specifically areas warming quicker) contributing strongly to spatial synchrony. The increase in spatial synchrony driven by temporal change in environmental conditions suggests that environmental change may relate to metapopulation extinction risk [**?**]. Understanding the spatial distribution of the rate of environmental change, and identifying the important environmental drivers of synchrony – scaling from single sites to entire metapopulations – is therefore an important research need. Given that rates of climate change are expected not only to continue but to accelerate, and even more so for higher latitudes, environmental forcing is likely to strongly affect synchrony networks in the future, potentially impacting community structure and demographic processes.

Tables

Table 1: Linear mixed effects models examining the effects of mean temperature and precipitation on two measures of centrality – strength (marginal R^2=0.53) and eigenvector (marginal R^2=0.58) – which estimate the importance of a given site to mean synchrony in moth populations. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	mean precipitation	-0.007	0.002	61	-3.08	**0.0031**
	mean temperature	-0.043	0.007	61	-6.22	$<$ **0.0001**
	sampling effort	0.001	0.0004	61	2.09	**0.0410**
Eigenvector	mean precipitation	-0.0001	$2.3e^{-5}$	61	-3.29	**0.0017**
	mean temperature	-0.0005	$7.3e^{-5}$	61	-7.07	$<$ **0.0001**
	sampling effort	$1.2e^{-5}$	$4.3e^{-6}$	61	2.84	**0.0061**

Table 2: Linear mixed effects models examining the effects of temporal change in temperature and precipitation on two measures of centrality – strength (marginal R^2=0.20) and eigenvector (marginal R^2=0.21) – which estimate the importance of a given site to mean synchrony in moth populations. Synchrony estimates were standardized by the number of significant synchrony links between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	precipitation	0.025	0.076	61	0.32	0.7483
	temperature	0.587	0.178	61	3.31	**0.0016**
	sampling effort	-0.0002	0.001	61	-0.47	0.6416
Eigenvector	precipitation	0.0001	0.0005	61	0.09	0.9295
	temperature	0.007	0.002	61	3.57	**0.0007**
	sampling effort	$-5.2e^{-7}$	$5.7e^{-6}$	61	-0.10	0.9243

Figures

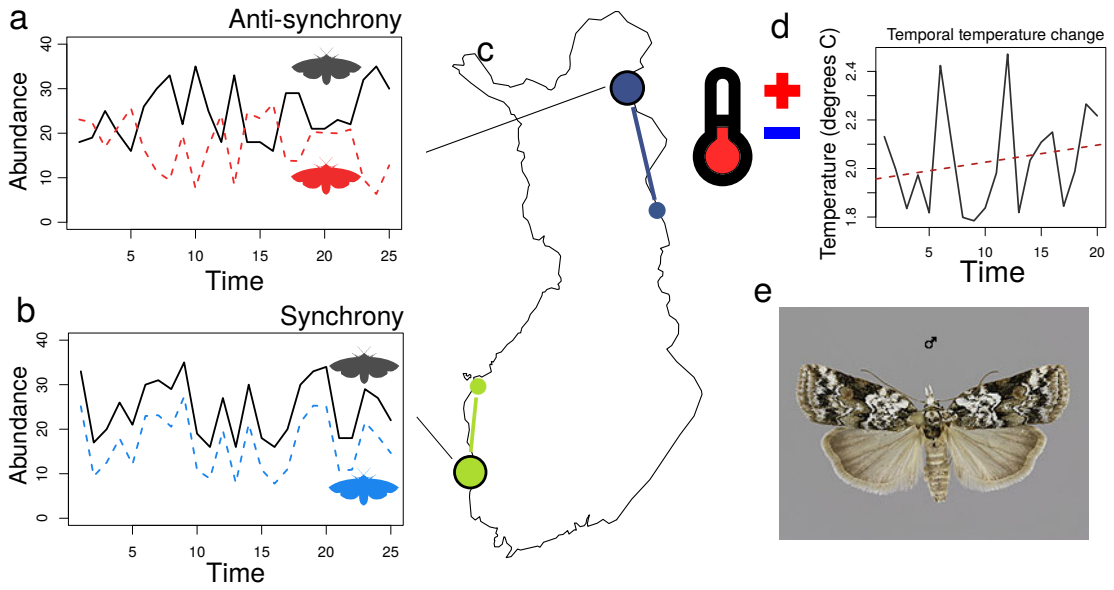

Figure 1: For each shared species between any pair of sites, a time series correlation was calculated. Significant negative and positive correlations ($\alpha = 0.05$) – corresponding to anti-synchronous (**a**) and synchronous (**b**) dynamics – were averaged across shared species between pairs of sites in order to quantify link strength. This created one synchrony and one anti-synchrony network, which were combined to create a single synchrony network spanning the entire country of Finland (**c**). Site-level synchrony values were then related to estimates of mean and temporal variation in environmental change (**d**) to understand spatial variation in site-level synchrony. A representative Finnish moth species is pictured in panel *e*.

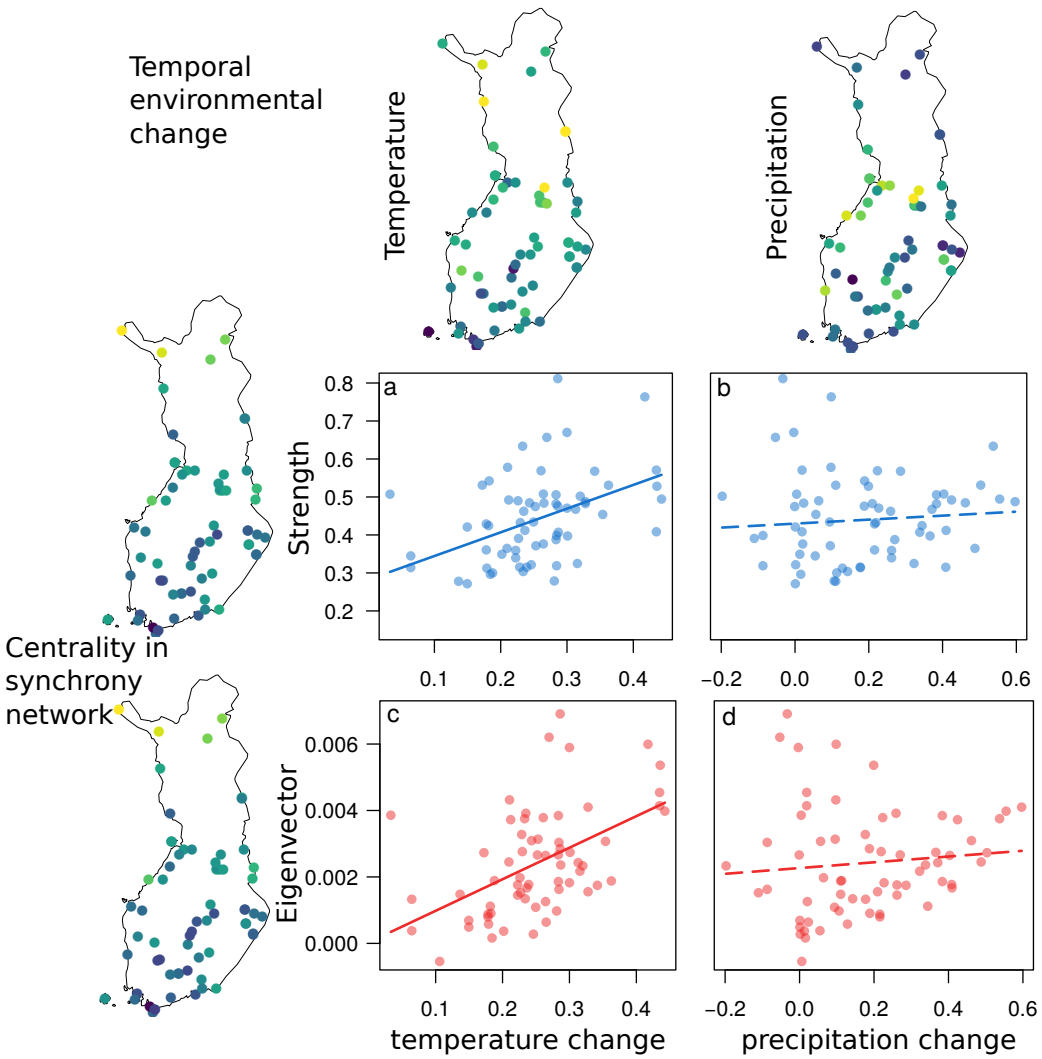

Figure 2: Site-level contributions to the synchrony network in terms of strength (panels *a* and *b*) and eigenvector (panels *c* and *d*) centrality, as a function of temporal change in temperature and precipitation. Maps show the spatial distribution of centrality estimates and temporal change in temperature and precipitation, with warmer (more yellow) colors indicating larger values. Solid plotted lines indicate significant relationships between site-level contributions to the synchrony network and temporal patterns in temperature change, while dotted lines indicate non-significant relationships.

Supplemental Material

Spatial synchrony is related to environmental change in Finnish moth communities

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Distance decay in synchrony

Sites with more nearby sites may have higher synchrony values as a function of spatial proximity to other sites and not due to a true spatial gradient in site-level contributions to spatial synchrony. That is, more distant sites should, on average, have lower synchrony values due to the increasing spatial distance between these distant sites and more clustered sites. However, this intuitive prediction would actually lead to opposite patterns relative to what we observed. The sites in the northern region of Finland – which have a larger average distance to other habitat patches – contribute strongly to the synchrony network. Here, we explore the effect of distance between sites and their average synchrony value. We do this by comparing the slope of the relationship between synchrony and spatial distance between every pair of sites to a null distribution, which shuffles site position while maintaining community composition. This randomization procedure was used to account for the non-independence of the pairwise data, providing a clearer test of the relationship between distance and synchrony. Significance was assessed by comparing the empirical distance-synchrony slope to a null distribution of 1000 randomized slope values using a z-test.

We find that the empirical distance-synchrony slope (b = -0.0303) was significantly more negative than expected relative to the null distribution (z = 2.97, p = 0.003), suggesting that spatial distance was related to the degree of synchrony. This does not preclude any of the causal mechanisms underlying synchronous relationships, as dispersal, spatially-autocorrelated environmental conditions, or a widespread mobile predator, all could be responsible for this relationship.

Positive and negative synchrony values among site pairs

In the main text, we construct 2 networks of spatial synchrony, where links connecting sites indicate the strength of synchrony or anti-synchrony for the average species present at both sites. While difficult to visualize effectively, we attempt to clarify our approach by plotting the synchrony and anti-synchrony networks (Figure **??**).

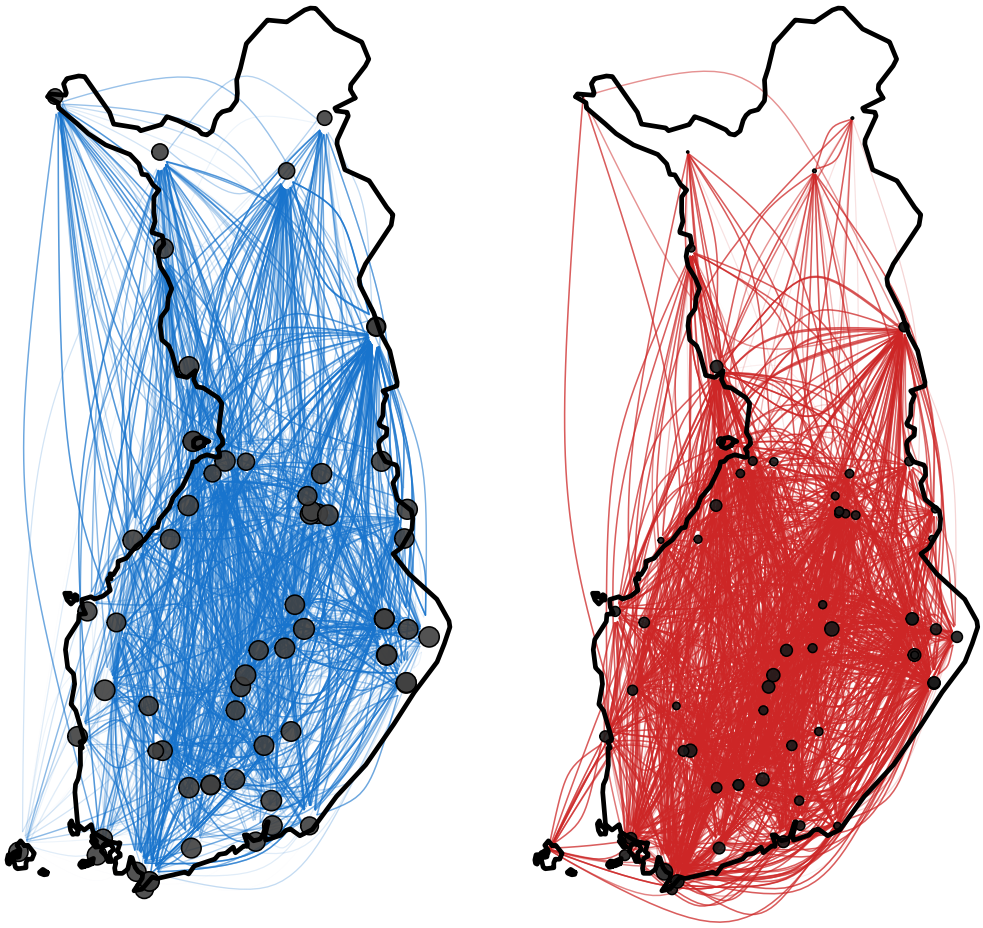

Figure S1: Positive (left panel in blue) and negative (right panel in red) mean correlations between species population dynamics for every combination of sites, where only significant links are included in the estimation of mean pairwise synchrony. This creates two spatial networks corresponding to representations of synchrony (left) and anti-synchrony (right). Link transparency is proportional to correlation strength, and point size corresponds to site-level contribution to spatial synchrony, estimated using weighted degree centrality (i.e., strength).

Shared sampling years among all pairs of sites

We used species time series correlations as a measure of synchrony for any given pair of sites. But spatial sampling was unequal i.e., not all sites were sampled every year. To account for this, we included the number of years each site was sampled as a covariate in the model. Here, for clarity, we also plot out the number of shared years for each pair of sites (Figure **??**). The robustness of our findings when considering the monthly and annual timescales suggests that sampling effort is not driving the observed patterns of synchrony.

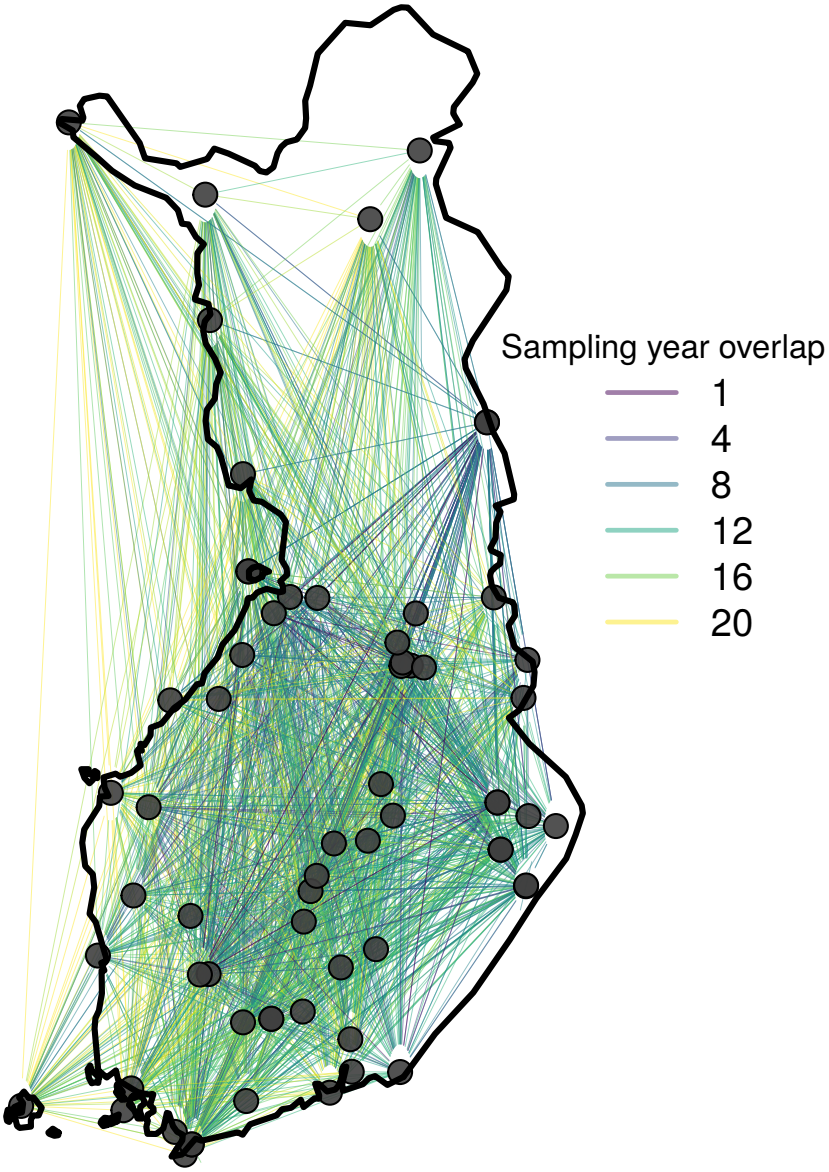

Figure S2: Sampling sites across Finland, linked by the number of shared sampling years between each pair of sites.

Community dynamics across the latitudinal gradient

It has been suggested that species demography – particularly high amplitude cyclic population dynamics – occurs more often at higher latitudes [**?**]. This is potentially due to environmental gradients and species-specific responses to these gradients. To provide a clearer view of the community dynamics at an annual timescale (the timescale used in our main text analyses), we visualize community dynamics for three sites across the latitudinal gradient of Finland (Figure **??**). While there are pronounced fluctuations, where certain species with low abundance in one year suddenly have large abundance in another, there is nothing to suggest that more northern populations are more or less periodic in their dynamics. In fact, at the annual timescale, it does not appear that many species adhere to any inter-annual periodicity (Figure **??**).

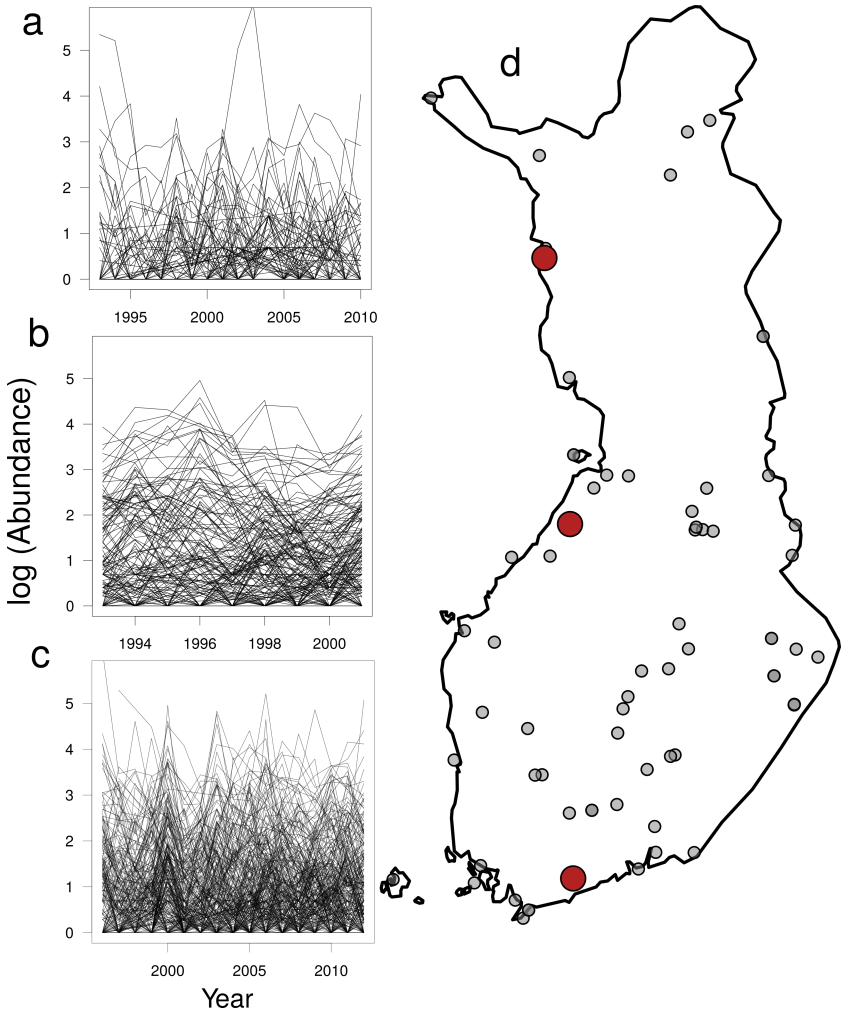

Figure S3: Community dynamics at annual timescales, where each line corresponds to a sampled species. Sites were selected based on their latitudinal position (mapped as red points on the map of Finland in panel d), in an effort to more clearly demonstrate the spatio-temporal dynamics at higher (a), more central (b), and more southern (c) latitudinal sampling points in Finland (d).

Sites contributing strongly to synchrony and anti-synchrony are the same

Site-level contributions to spatial synchrony – estimated using centrality measures that combine the mean pairwise correlations of species dynamics between sites – may identify different spatial hotspots of sites contributing strongly to synchrony and anti-synchrony networks. This could help identify the drivers of synchrony, as spatial variation in environmental conditions or mobile predator density could be related to the degree of synchrony(anti-synchrony). We find that sites contributing strongly to synchrony were the same sites contributing strongly to anti-synchrony (Figure **??**). While this relationship may be influenced by species richness or shared diversity between sites, it persists after standardizing correlation coefficients by the number of significant links between sites (Figure **??**).

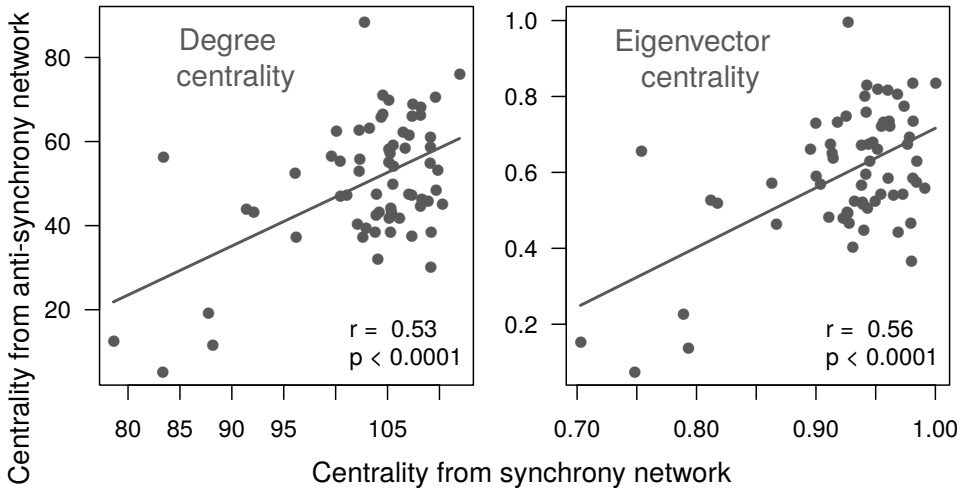

Figure S4: Sampling sites with large positive(synchrony) or negative(anti-synchrony) mean correlations tended to be the same sites, resulting in positive correlations between site-level contributions to spatial synchrony, quantified using strength centrality (left panel) and eigenvector centrality (right panel). In order to calculate anti-synchrony values, we took the absolute value of the pairwise synchrony links between sites. This suggests that communities are not wholly synchronous or anti-synchronous, but species dynamics between sites contain a balance of both synchrony and anti-synchrony.

Effects of standardizing links by degree centrality

In the main text, we standardized centrality values of each site in our synchrony networks based on the number of links they had with other sites. This was performed because sites connected with a greater number of sites would naturally tend to have higher centrality values. The standardization of centrality by the number of connections each node has – where connections represent mean synchrony values across all shared species between the two sites – penalizes nodes that share many species, or that, due to spatial proximity or other factors, have a large number of synchronous links with other sites. Here, we remove this standardization attempt, calculating site-level centrality measures without any correction. Mean values of temperature and precipitation were related to site-level values of synchrony, quantified as strength and eigenvector centrality, and measured at both monthly (Table **??**) and annual (Table **??**) timescales. We find the same tendency for temporal temperature change to be positively related to strength and eigenvector centrality at both monthly (Table **??**) and annual (Table **??**) timescales, providing further support for the robustness of our main text findings.

Table S1: Linear mixed effects models examining relationships between mean temperature and precipitation to two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations. Site-level synchrony estimates were based on calculating synchrony at the monthly timescale, with links not standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	mean precipitation	-0.324	0.21	61	-1.53	0.1315
	mean temperature	-4.488	0.67	61	-6.66	$<$ **0.0001**
	sampling effort	0.122	0.04	61	3.05	**0.0034**
Eigenvector	mean precipitation	-0.007	0.00	61	-2.50	**0.0150**
	mean temperature	-0.070	0.01	61	-7.71	$<$ **0.0001**
	sampling effort	0.002	0.00	61	3.81	**0.0003**

Table S2: Linear mixed effects models examining relationships between mean temperature and precipitation to two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations, calculated at the annual scale, with links not standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	mean precipitation	-0.544	0.26	61	-2.11	**0.0391**
	mean temperature	-4.592	0.82	61	-5.61	$<$ **0.0001**
	sampling effort	0.166	0.05	61	3.40	**0.0012**
Eigenvector	mean precipitation	-0.007	0.00	61	-2.66	**0.0099**
	mean temperature	-0.056	0.01	61	-6.62	$<$ **0.0001**
	sampling effort	0.002	0.00	61	3.64	**0.0006**

Table S3: Linear mixed effects models examining relationships between temporal temperature and precipitation change to two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations. Site-level synchrony estimates were based on calculating synchrony at the monthly timescale, with links not standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	precipitation	12.873	6.56	61	1.96	0.0544
	temperature	69.499	14.96	61	4.65	$<$ **0.00001**
	sampling effort	0.034	0.04	61	0.96	0.3433
Eigenvector	precipitation	0.135	0.10	61	1.33	0.1899
	temperature	1.013	0.23	61	4.38	$<$ **0.00001**
	sampling effort	0.000	0.00	61	0.95	0.3476

Table S4: Linear mixed effects models examining relationships between temporal temperature and precipitation change to two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations. Site-level synchrony estimates were based on calculating synchrony at the annual timescale, with links not standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	precipitation	8.393	8.05	61	1.04	0.3010
	temperature	72.454	18.72	61	3.87	**0.0003**
	sampling effort	0.069	0.05	61	1.33	0.1884
Eigenvector	precipitation	0.057	0.09	61	0.63	0.5335
	temperature	0.839	0.21	61	3.99	**0.0002**
	sampling effort	0.001	0.00	61	0.99	0.3256

Removal of a known cyclic species

Species that exhibit multi-annual cycles may lead to strong synchronous population dynamics through phase-locking. This is admittedly a very minor concern, since in order for this to influence the analyses, all species between two communities would need to be phase-locked, which is extraordinarily unlikely. Here, we examine the influence of the removal of one such species which was expected to have the largest impact on our results, *Epirrita autumnata*. This species exhibits multi-annual cyclic population dynamics, can reach very high abundances (this doesn't impact our analyses, but is interesting to note), and is distributed more in northern sites. We removed this species from the analyses, and saw that there was almost zero effect on our overall results for both the relationship between centrality in synchrony networks and mean conditions (Table **??**) or temporal environmental change (Table **??**). Therefore, our results are not being driven by the differential distribution of phase-locking species.

Table S5: Linear mixed effects models examining the effects of mean temperature and precipitation on two measures of centrality – strength (marginal $R^2 = 0.52$) and eigenvector (marginal $R^2 = 0.57$). A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort. Here, we excluded *Epirrita autumnata*, a species known to be distributed more in the northern sites and known to experience multi-annual cyclic population dynamics.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	mean precipitation	-0.007	0.00	61	-3.07	**0.0032**
	mean temperature	-0.043	0.01	61	-6.11	$<$ **0.0001**
	sampling effort	0.001	0.00	61	2.13	**0.0373**
Eigenvector	mean precipitation	-0.0001	$2.3e^{-5}$	61	-3.27	**0.0018**
	mean temperature	-0.0005	$7.4e^{-5}$	61	-6.95	$<$ **0.0001**
	sampling effort	$1.3e^{-5}$	$4e^{-6}$	61	2.86	**0.0059**

Table S6: Linear mixed effects models examining the effects of temporal change in temperature and precipitation on two measures of centrality – strength (marginal R^2=0.20) and eigenvector (marginal R^2=0.21). Synchrony estimates were standardized by the number of significant synchrony links between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort. Here, we excluded *Epirrita autumnata*, a species known to be distributed more in the northern sites and known to experience multi-annual cyclic population dynamics.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	precipitation	0.027	0.077	61	0.35	0.7262
	temperature	0.581	0.179	61	3.24	**0.0020**
	sampling effort	-0.0002	0.001	61	-0.42	0.6777
Eigenvector	precipitation	0.0001	0.0008	61	0.24	0.8978
	temperature	0.007	0.002	61	3.50	**0.0009**
	sampling effort	$-5e^{-7}$	$5.1e^{-6}$	61	-0.06	0.9505

Effect of temporal sampling scale

In the main text, we estimated site-level synchrony from samples taken at the annual scale. This was due to the potential for seasonality to lead to fluctuations in population dynamics, which may bias the correlations and resulting synchrony values. However, this also serves to limit the number of samples used to estimate synchrony. Here, we use data on monthly mean moth abundances to explore the effect of temporal scale on the relationship between site centrality in our synchrony networks and temporal variation in temperature and precipitation.

Our findings were insensitive to temporal sampling scale (Table **??** and **??**). Synchrony networks tended to be quite similar structurally (Figures **??** and **??**). Specifically, a majority of links in the annual networks were conserved in the monthly networks for synchrony (94% of links overlap), but to a far lesser extent for anti-synchrony (38% of links overlap). This further supports the robustness of our main text findings with respect to the relationship between temporal environmental variation and site-level synchrony values based on strength and eigenvector centrality (Figure **??**).

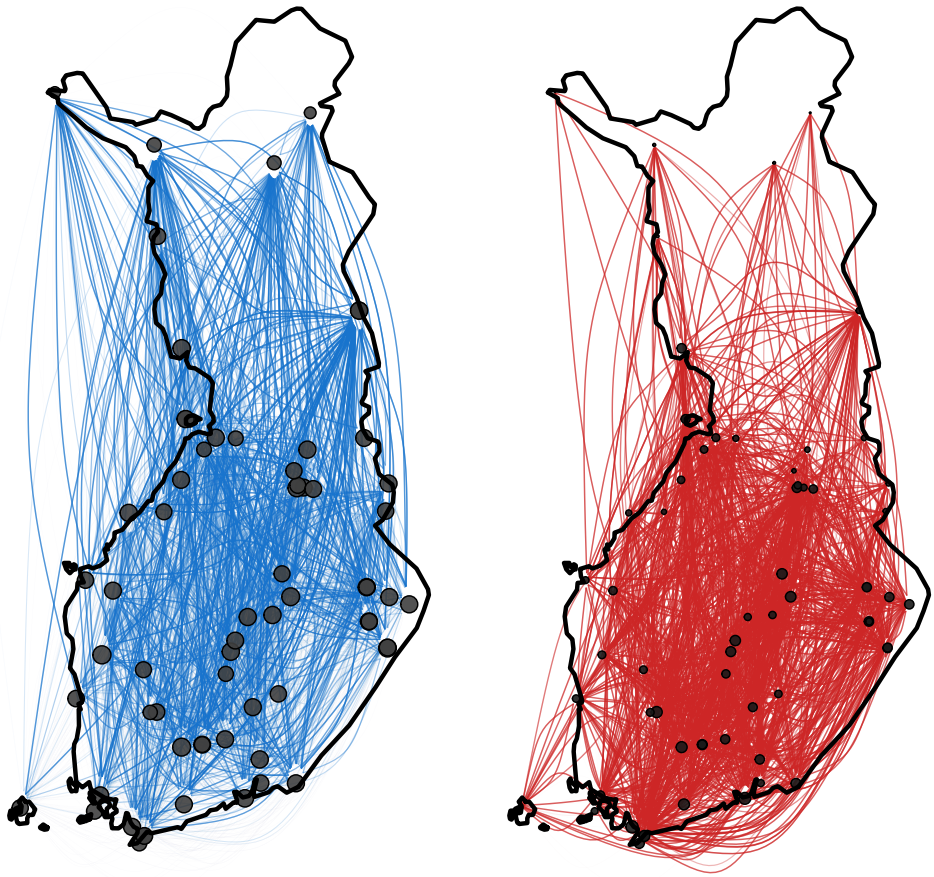

Figure S5: Positive (left panel in blue) and negative (right panel in red) correlations between time series of every combination of sites (link transparency is proportional to correlation strength) calculated on a monthly timescale, and point size corresponds to site-level contribution to spatial synchrony, estimated using weighted degree centrality (i.e., strength).

Table S7: Linear mixed effects models examining the effects of mean temperature and precipitation on two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations, taken at the monthly timescale, with links standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	mean precipitation	-0.006	0.00	61	-3.32	**0.0015**
	mean temperature	-0.048	0.01	61	-8.74	$<$ **0.0001**
	sampling effort	0.001	0.00	61	2.14	**0.0366**
Eigenvector	mean precipitation	-0.000	0.00	61	-3.51	**0.0009**
	mean temperature	-0.001	0.00	61	-9.06	$<$ **0.0001**
	sampling effort	0.000	0.00	61	3.50	**0.0009**

Table S8: Linear mixed effects models examining the relationship between temporal change in temperature and precipitation to two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations, with links standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort. Temporal change in temperature and precipitation were both positively and significantly related to the two measures of site-level contribution to synchrony.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	precipitation	0.030	0.07	61	0.41	0.6836
	temperature	0.630	0.16	61	3.89	**0.0003**
	sampling effort	-0.000	0.00	61	-0.85	0.4013
Eigenvector	precipitation	0.000	0.00	61	0.37	0.7115
	temperature	0.009	0.00	61	3.98	**0.0002**
	sampling effort	0.000	0.00	61	0.12	0.9031

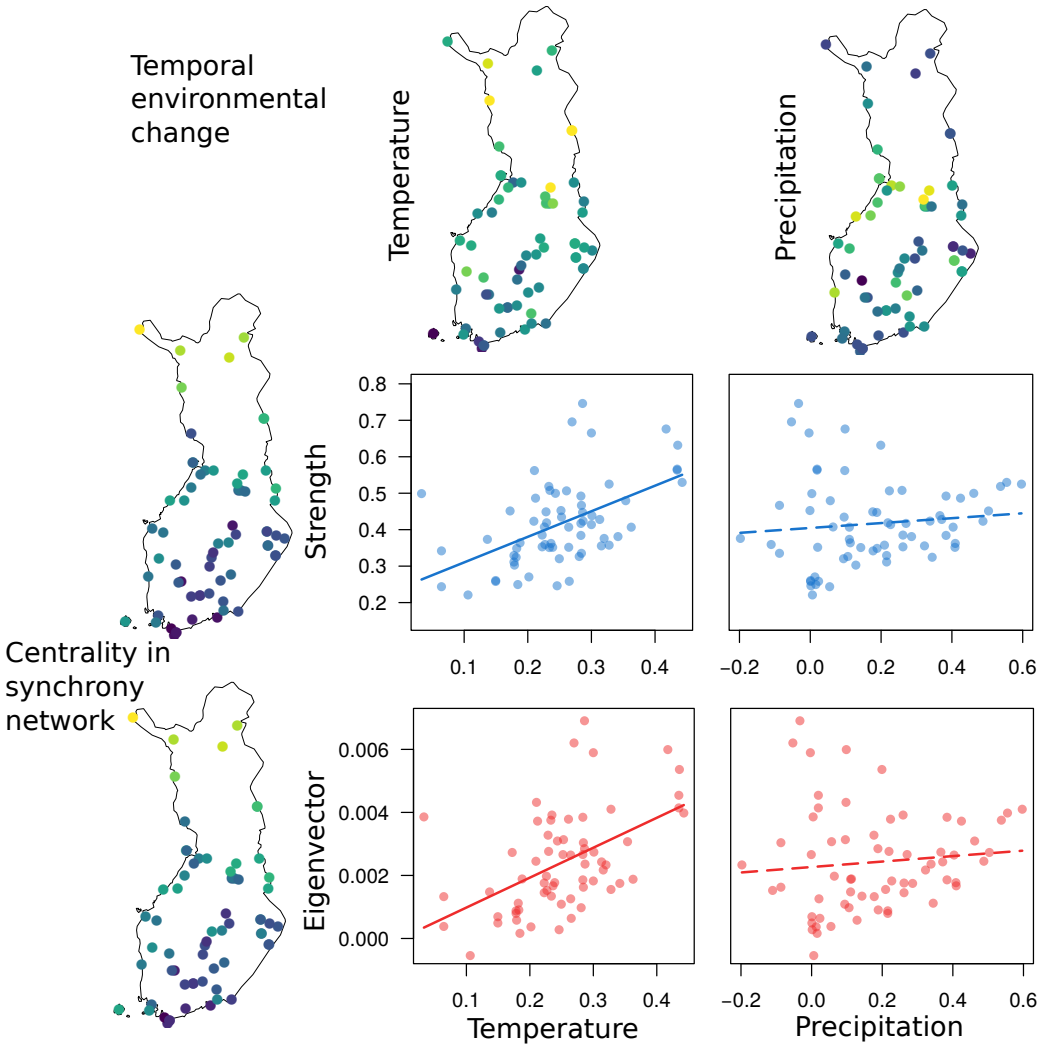

Figure S6: Site-level contributions to the synchrony network in terms of strength (top panel) and eigenvector (bottom panel) centrality, as a function of temporal change in temperature and precipitation. Synchrony was calculated using monthly mean estimates of moth abundance, as opposed to the annual means used in the main text. Maps show the spatial distribution of centrality estimates and temporal change in temperature and precipitation, with warmer (more yellow) colors indicating larger values. Solid plotted lines indicate significant relationships between site-level contributions to the synchrony network and temporal temperature change, while dotted lines indicate non-significant relationships.

Considering all correlations to estimate edgeweights

In the main text, we exclude non-significant correlations between pairs of sites before calculating the mean synchrony values. Here, we include all correlation coefficients in the calculation of the mean, which serves to add noise and drive the mean value towards zero. While this qualitatively supports many of the main text findings, there are some small differences compared to the other analyses (e.g., the analyses in the sections "Effects of standardizing by centrality", "Removal of a known cyclic species", and "Effect of temporal sampling scale"). For instance, the importance of mean temperature to site-level estimates of synchrony remains similar (Table **??**), but the influence of precipitation is not observed in the mean climate models. The loss of statistical significance when considering all correlations to quantify pairwise synchrony values could be a function of tendency of non-significant correlations to be near zero. This serves to add a layer of noise over the significantly synchronous (or anti-synchronous) relationships.

Table S9: Linear mixed effects models examining the effects of mean temperature and precipitation on two measures of centrality – strength (marginal R^2=0.53) and eigenvector (marginal R^2=0.58) – which estimate the importance of a given site to mean synchrony in moth populations. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	mean precipitation	-0.000	0.00	61	-0.73	0.4692
	mean temperature	-0.006	0.00	61	-3.57	**0.0007**
	sampling effort	0.000	0.00	61	1.98	0.0528
Eigenvector	mean precipitation	0.000	0.00	61	0.43	0.6656
	mean temperature	-0.000	0.00	61	-0.87	0.3850
	sampling effort	0.000	0.00	61	3.36	**0.0014**

Table S10: The results change slightly when all correlation coefficients are considered, potentially due to the added noise from non-significant relationships. Linear mixed effects models examining the relationship between temporal change in temperature and precipitation to two measures of centrality (strength and eigenvector) which estimate the importance of a given site to mean synchrony in moth populations, with links standardized by the number of shared species between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

Centrality measure	Variable	Estimate	SE	DF	t	p
Strength	precipitation	0.004	0.02	61	0.27	0.7904
	temperature	0.055	0.04	61	1.51	0.1371
	sampling effort	0.000	0.00	61	0.67	0.5026
Eigenvector	precipitation	0.002	0.00	61	1.44	0.1556
	temperature	0.001	0.00	61	0.35	0.7312
	sampling effort	0.000	0.00	61	3.44	**0.0010**

Environmental change in Finland

As a secondary product of the main text analyses, we produced high-resolution (1 km^2) maps of the rates of change – quantified as Spearman's rank correlations of each square km over time – in temperature (Figure **??**) and precipitation (Figure **??**) from the period between 1990 and 2013.

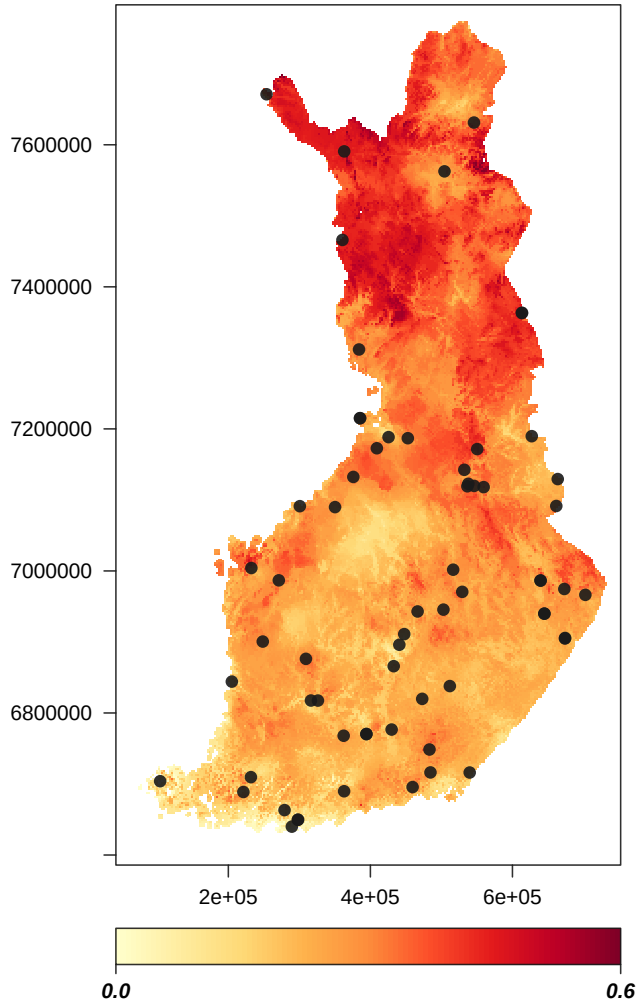

Figure S7: Temporal change in temperature – measured as the Spearman's correlation coefficient – from 1990 to 2013 in Finland, based on monthly average temperature values. Moth community sampling sites are plotted as black points.

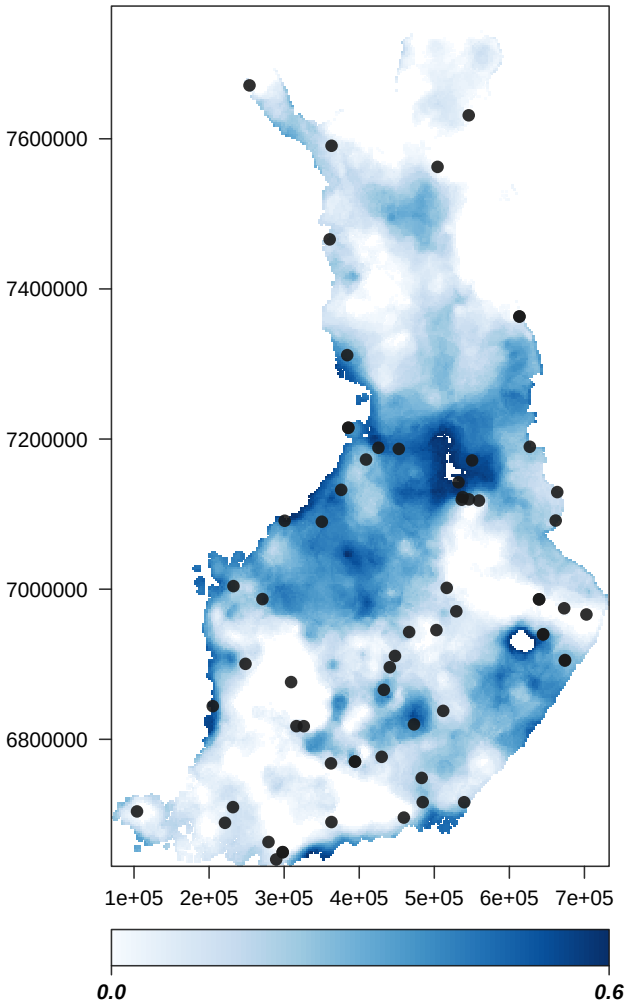

Figure S8: Temporal change in precipitation – measured as the Spearman's correlation coefficient – from 1990 to 2013 in Finland, based on monthly average precipitation values. Moth community sampling sites are plotted as black points.